RESPONSE OF BARLEY LEAF AND TILLER GROWTH AND DEVELOPMENT TO PHOTOPERIOD

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ABSTRACT

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Tiivistelmä — Referat — Abstract

The growth and development of barley (*Hordeum vulgare* L.) is affected by photoperiod and temperature. Photoperiod has various signalling functions affecting reproductive development and its rate. It also affects the rates of leaf area extensions and dry matter production. Increase in photoperiod hastens the plant developmental processes and affects the leaf area and tiller formation. Primary tillers form from axillary buds in the leaf nodes on the main culm and increase the leaf area of the plant. Under favourable conditions, initiated tillers grow to separate culms with grain bearing ears. However, the environmental conditions during the growing season in northern latitudes affect tiller formation. The aims of the experiments were to investigate the effects of photoperiod on barley leaf and tiller development. Other aims were to compare the differences expressed by the two row-types and tillering habits.

Seven barley accessions, differing in tillering habit and row-type, were used in the experiments. Three pairs of near-isogenic accessions six-rowed 'Morex' and 'Uniculm Morex', 'Kindred' and 'Uniculm Kindred', two-rowed 'Ingrid' and '3-503', differing in tillering habit, and two-rowed 'Saana' were grown in growth chamber at humidity of 60/70 % and at temperature 18/12 ºC (day/night), in three different photoperiods (15 h, 18 h and 21 h). The leaf length and width were measured from the full-grown leaves. The samples to identify main culm and tillers were taken after the plants reached the 4-leaf-stage. The effects of photoperiod, accession, tillering habit and row-type on the plant, leaf and tiller growth were statistically analysed.

Increase in photoperiod hastened the plant development as well as leaf and tiller emergence rates. The leaf size and main culm leaf area decreased as the photoperiod increased. The number of tillers increased as photoperiod increased. The uniculm accessions had larger leaves and a larger main culm leaf area than the conventional tillering accessions. Six-rowed accessions had larger leaves and a larger main culm leaf area than the two-rowed accessions. The two-rowed accessions had a faster tiller emergence rate and a higher tiller number compared to the six-rowed accessions.

Photoperiod treatments affected the leaf and tiller growth and development as expected apart from the number of tillers produced in the longest, 21h photoperiod. Differences between the two tillering habits and row-types were also as expected, although some exceptions occurred. Potentials and limitations of uniculm growth habit in agricultural production were also discussed.

Avainsanat — Nyckelord — Keywords

Hordeum vulgare, photoperiod, growth, leaf, tiller, tillering, leaf area, uniculm, row-type

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Muita tietoja — Övriga uppgifter — Further information

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ABBREVATIONS AND CONCEPTS

HI – harvest index

LAI – leaf area index

PAR – photosynthetically active radiation

TC – coleoptile tiller

T1–T6 – primary tillers from first to sixth leaf node

1 INTRODUCTION

Barley (genus *Hordeum*) is one of the ancient crops that have had a role in human development (Ullrich 2011). It was among the first domesticated crop species and has been widely utilized around the world both as human food and animal feed (Baik and Ullrich 2008, von Bothmer and Komatsuda 2011, Ullrich 2011). Cultivated barley (*Hordeum vulgare* L.), which belongs to *Poaceae* family, is adapted to temperate and semiarid subtropical climates (Ullrich 2011). Regardless of its wide adaptation to drought and cold, barley does not, however, tolerate humid and hot climates (Ullrich 2011).

Growth and development of temperate cereal species, like barley, are affected by temperature, and in some instances, daylength (Hay 1990, McMaster 2005). Many of these species are adapted to long daylength (over 13 h), or in other terms, to long-day photoperiod, in which case the photoperiod has important signalling functions. Photoperiod can act as a signal to initiate the reproductive development, it can influence the rate of reproductive development after it is initiated, and cause changes in the rate of leaf area extension as well as dry-matter production (Hay 1990). However, the photoperiod insensitive varieties of barley and wheat (*Triticum aestivum* L. emend Thell.) do not need the photoperiod signalling to initiate the reproductive development (Law et al. 1978, Buck-Sorlin and Börner 2001).

Cereal canopies are built from defined structural units known as the phytomers. Single phytomer consists of a leaf and leaf associated node, internode and axillary bud (McMaster 2005). Canopies are formed as phytomers continuously form, expand and senescence (McMaster 2005). In cereal leaves, the expansion zone at the lamina base is short and the cells on the leaf surface do not divide after the leaf has emerged (Dale 1988). Thus the individual cereal leaf's blade that emerges from the leaf sheath bundle, is fully expanded and the leaf only elongates in length and not in width (Dale 1988, Bos and Neuteboom 1998). The leaf emergence rate and leaf size are controlled by genetic characteristics, environmental factors such as temperature and light intensity, and farming practices (Kirby et al. 1985a, Kirby et al. 1985b, Bos and Neuteboom 1998). However, the individual leaves only form a part of the total canopy structure and, for example tillers, also affect the structure of the canopy. Genetics, environmental factors, and different

farming practices affect the formation and the structure of the crop canopy (Bos and Neuteboom 1998, Buck-Sorlin and Börner 2001, Prystupa et al. 2003).

In cereal plants, tillers are formed from axillary buds in coleoptilar node and from the nodes of the lower leaves (Hay and Kirby 1991, McMaster 2005, Rebetzke et al. 2008). The tiller buds initiate and grow to produce stems, or culms, with productive ears under favourable conditions. The early growth of tillers contributes to the increase in ground cover, which in turn increases the light interception capacity of the plant and eases the competition against weeds (Jewiss 1972, Lemerle et al. 1996, Rebetzke et al. 2008). Tiller development is controlled by various factors, such as genotype and environmental conditions. Different management practices can be used to control the tillering, for example high plant density and nutrient fertilization (Kirby and Faris 1972, Prystupa et al. 2003). The tillers also contribute to the total leaf area of a crop plant in the later developmental stages (Kirby et al. 1982).

Plants capture most of the energy needed for photosynthesis and carbon assimilation via green leaf area, although other green plant parts, such as the ear and flag leaf sheath, contribute to the energy harvest as well (Repková et al. 2009). The energy captured in the green plant parts is then converted into biomass, and distributed among different sinks, such as developing leaves and maturing ear, during different developmental stages (Peltonen-Sainio et al. 1997). The ratio of the green leaf laminae area to the ground area is a commonly used parameter and known as the leaf area index (LAI) (Peltonen-Sainio et al. 1997). The size of the plant's LAI describes its ability to capture the photosynthetically active radiation (PAR). Where LAI is above optimum, from three to five in cereals, the upper green leaves start to shade the lower canopy (Peltonen-Sainio et al. 1997). Shading alters the amount of PAR entering the lower parts of the canopy which reduces the photosynthesis and affects the formation and survival of tillers (Kirby and Faris 1972, Lauer and Simmons 1989, Peltonen-Sainio et al. 1997, Evers et al. 2006).

Donald (1968) outlined a wheat ideotype that would produce a high grain yield with minimum use of resources. The ideotype would also have a high harvest index (HI), meaning that the produced grain yield relative to the total produced biomass is high. Similar objectives can be applied to other temperate cereals, such as barley. The said ideotype would, among various other characteristics, have one strong and short culm, few

erect leaves and a large ear (Donald 1968). The leaves of independent crops should be erect, few in number and small, since the upper leaves on the culm shadow the lower leaves and reduce the amount of light that can reach the lower parts of the canopy. Low light intensity reduces the photosynthesis and carbon assimilation in the leaves that are located lower on the main culm (Donald 1968). Having few leaves on the main culm maximises the leaf area but minimises the shading effect. Erect leaves are generally smaller in size than the more horizontal leaves (Donald 1968).

In wheat ideotype, the single plant should have only one short and sturdy culm. Short stem has the advantage to prevent lodging at harvest and it also affects the leaf positioning on the stem (Donald 1968). The single culm growth habit, or the uniculm growth habit, is considered to have also other advantages compared to the conventional tillering growth habit. The tillers that fail to produce ears or produce ears that mature later than the main ear, can be regarded as wasteful use of resources in terms of yield production and yield quality (Donald 1968, Kirby and Jones 1977, Peltonen-Sainio et al. 2009). Tillering is thus, for many reasons, considered a disadvantageous trait in cereal crop production, although in some cases the tillers can also be beneficial to the total yield production. For example, in a case where the main culm is lost for some reason, the tillers may replace it and thus provide to the total yield production (Alaoui et al. 1988).

In northern latitudes, the growing season is short and relatively cold, and it is affected by long day conditions (Mukula and Rantanen 1986). These characteristics provide the framework in which the agricultural production is practiced. Long day conditions inhibit the tiller formation and common early summer droughts suppress the tillering in early developmental stage in spring cereals (Peltonen-Sainio et al. 2009). The early season suppression of tillering may also lead to tillering in later developmental stage, which combined with late-season rainfall, negatively affects the harvest itself and the quality of the yield (Peltonen-Sainio et al. 2009). The uniculm growth habit has been proposed as a potential solution for a more stable yield in the northern production areas (Balkema-Boomstra and Mastebroek 1993).

As the northern latitudes set diverse environmental settings for plant growth, the aim of this work was to investigate the effects of different long-day photoperiods on barley leaf and tiller development. Other aims were to compare the effects of uniculm growth habit

to the conventional tillering growth habit and differences expressed by the two row-types in leaf and tiller development.

2 LITERATURE REVIEW

2.1 Plant development in spring wheat and barley

2.1.1 Plant development

Plant development should be distinguished from plant growth. Plant growth is merely accumulation of dry matter whereas developmental processes include production, differentiation, expansion, and the loss of phytomers (McMaster 2005). The plant development in cereal crops, such as wheat and barley, can be divided into vegetative and generative stages (Bonnett 1966). During the vegetative stage leaf initials form in the shoot apex and tiller development is active (Bonnett 1966). The transition from vegetative to generative stage is marked by the formation of the double ridge on the shoot apex (Figure 1). An upper part of the double ridge transforms to spikelet primordium (Bonnett 1966).

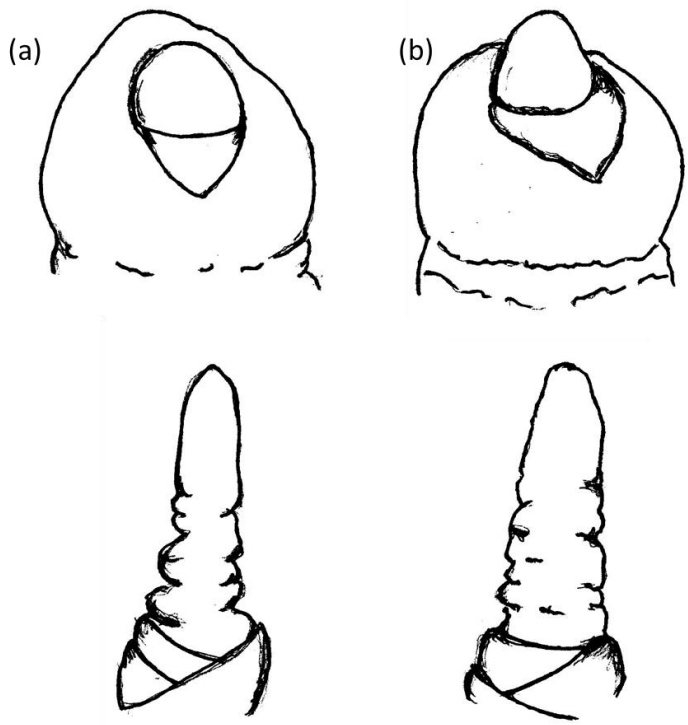

Figure 1. Vegetative and generative phase of barley (a) and wheat (b) apex primordia. Not in scale. (Drawn by H. Bäckström).

2.1.2 Photoperiod effect on plant development rate

Guitard (1960) showed that long day (16 h and 24 h) affected the time needed for the development of barley from sowing to heading by reducing it. Similarly in wheat, the long photoperiod (16–21 h) accelerated the plant development (Davidson et al. 1985, Evans and Blundell 1994, Slafer and Rawson 1996). According to Aspinall (1966), in barley the rate of apex primordium production was higher in the longer photoperiods (16 h and 24 h) but the number of primordia that was produced was smaller. Increase in photoperiod also led to more rapid double ridge formation and floral development (Aspinall 1966). Slafer and Rawson (1996) found that daylength, among accessions and temperature, significantly affected the development from sowing to double ridge formation and from double ridge stage to terminal spikelet initiation. The short daylength (9 h and 12 h) decreased the development rate (Slafer and Rawson 1996). The effect of daylength was significant also in the development period from terminal spikelet initiation to heading, but the effect varied among the accessions (Slafer and Rawson 1996). The duration of the developmental stages from heading to maturity was longer in the long

photoperiod (16 h and 24 h) when the long days occurred in the early stage of plant development, from sowing to elongation of the internode (Guitard 1960). The longer photoperiod (16 h and 24 h) applied during the developmental stages from heading to maturity accelerated the plant development (Guitard 1960). Kernich et al. (1996) obtained similar results on barley and stated that long photoperiod (18 h) reduced the time needed for plant development from double ridge stage to awn primordia.

2.2 Leaf development in spring wheat and barley

2.2.1 Phyllochron and leaf development rate

Phyllochron is the time interval that is needed for successive leaves to emerge in cereals (Cao and Moss 1989b). Cao and Moss (1989b) discovered that temperature affects the phyllochron in barley and wheat. Phyllochron increased as the temperature increased (Cao and Moss 1989b). However, phyllochron is also affected by daylength, increase in which results in decrease in phyllochron (Cao and Moss 1989a).

Leaf development rate in barley and wheat is affected by temperature and daylength (Cao and Moss 1989a, Cao and Moss 1989b). Leaf development rate is faster in barley than in wheat (Cao and Moss 1989b, Miralles and Richards 2000). Increase in temperature led to increase in the leaf emergence rate (Cao and Moss 1989b). However, after achieving the optimum temperature, the rate of leaf emergence decreased as the temperature increased (Cao and Moss 1989b). Cao and Moss (1989a) observed that increase in daylength also increased the leaf emergence rates of wheat and barley. However, Evans and Blundell (1994) discovered that the decreasing effect of a shorter photoperiod (8 h) to wheat leaf emergence rate appeared only in the shorter photoperiods (8 h and 12 h).

Miralles and Richards (2000) discovered that transferring barley and wheat plants from one daylength to another affected the rate of leaf emergence. The plants were grown under 9 h, 13 h and 19 h photoperiods, and some of the plants were transferred to other photoperiods after wheat reached its terminal spikelet initiation and barley reached its triple mound (Miralles and Richards 2000). The leaf emergence rate increased as the

plants were moved from shorter photoperiod to longer photoperiod and decreased as the plants were moved to shorter photoperiod, except for moving wheat from 13 h photoperiod to 9 h photoperiod (Miralles and Richards 2000).

2.2.2 Leaf size and leaf area in wheat and barley

The individual barley or wheat leaf blade emerges from the sheath bundle and the extension zone, where emerging leaf is expanding, is relatively short (Dale 1988). The leaf blade increases only in length and not in width after the leaf emerges from the sheath bundle (Dale 1988, Bos and Neuteboom 1998). The leaf area is one of the main factors affecting the solar radiation interception in a single crop plant, although other green plant organs, such as the green ear, also contribute to the leaf area (Repková et al. 2009).

Aspinall and Paleg (1964) found that light intensity, rather than photoperiod, affected the leaf dimensions of barley. Williams and Williams (1968) showed that in wheat, the long photoperiod reduced the final leaf area, but according to Friend et al. (1967) long photoperiod (20 h and 24 h) increased the leaf area.

Pararajasingham and Hunt (1995) reported that photoperiod affected the length of the successive wheat leaves. In the short, 8 h photoperiod, the successive leaves were longer until sixth or seventh successive leaf depending on the accession (Pararajasingham and Hunt 1995). In longer photoperiods, the leaf length increased until fifth (12 h) or third successive leaf (16 h and 20 h) (Pararajasingham and Hunt 1995). According to Pararajasingham and Hunt (1995), leaf width increased as the leaf number increased. The short, 8 h photoperiod, resulted in the narrowest leaves, although the effect was generally notable only after the fifth leaf (Pararajasingham and Hunt 1995).

2.2.3 Main culm leaf number

According to Guitard (1960), in barley the leaf number of the main culm is affected by the daylength during the development of leaf primordia. The leaf number decreased with the increasing daylength (Guitard 1960). Friend et al. (1967) found that in wheat the total number of leaves present on plants after four weeks of growth increased as the daylength

increased from 8 h to 24 h. According to Kernich et al. (1996), in barley the long day (18 h) before the double ridge stage resulted in fewer leaves on the main culm than the short day (10 h). Miralles and Richards (2000) described the same effect of long photoperiod (19 h) in decreasing the final leaf number on the main culm in both barley and wheat. This decrease in the leaf number was due to the long photoperiod (19 h) during the vegetative phase of the plant development (Miralles and Richards 2000).

2.3 Tiller development in spring wheat and barley

2.3.1 Tillering in spring wheat and barley

For spring cereals in general, rapid tillering at the beginning of growth is a mean to increase the leaf area for intercepting light (Jewiss 1972). Early growth and tillering are an advantage in competition against weeds (Lemerle et al. 1996). However, barley tillers not surviving long enough to produce ears could be considered as a waste of resources (Kirby and Jones 1977). Furthermore, removing tillers enhanced the growth of an individual plant and its yield formation. Similar observations were done by Alaoui et al. (1988) on field conditions. However, Alaoui et al. (1988) also stated that rather than removing all the tillers, the number of tillers should be limited to a few surviving and yield bearing tillers. These few retaining tillers could compensate the possible loss of the main culm (Alaoui et al. 1988). Hucl and Baker (1991) observed that oligoculm growth habit in wheat was not optimal in stressful and semiarid conditions in Western Canada since the grain yields were lower than in the conventional tillering cultivars.

Tillers in spring cereals mostly occur in the main culm axis but coleoptile tillers grow from the underground coleoptilar node (Figure 2) (Thorne 1962, Rebetzke et al. 2008). The emergence and size of coleoptile tillers depend on genotype and environmental factors, such as temperature and soil conditions (Rawson 1971, Rebetzke et al. 2008). Kerbom et al. (2013) described the main culm tillers as basal and aerial tillers. Basal tillers grow from internodes at the base of the main culm that have not elongated (Kerbom et al. 2013). Aerial tillers, on the other hand, generally grow from elongated nodes from higher parts of the main culm and, unlike the basal tillers, aerial tillers are unable to survive the

death of the main culm (Kerbom et al. 2013). Tillering phase usually ends as vegetative growth changes to generative growth, and poorly established tillers start to senesce (Kerbom et al. 2013).

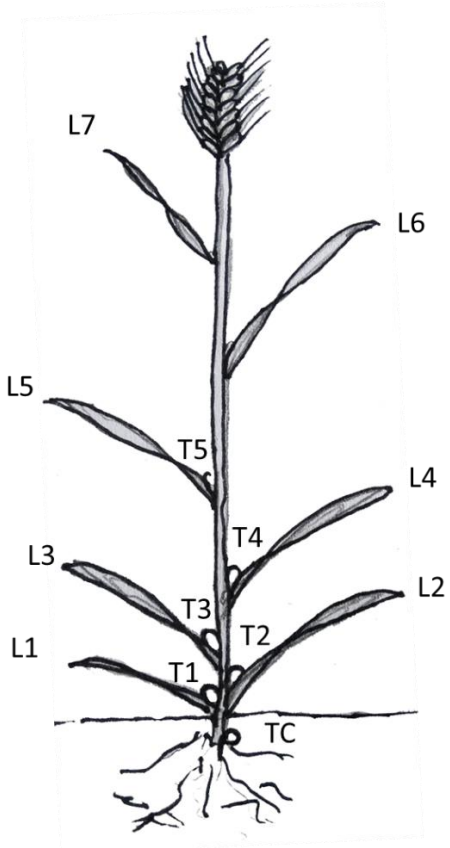

Figure 2. Generalized structure of a cereal plant. L1–L7 the leaves in emergence order, T1–T5 axillary buds for primary tillers, TC for coleoptilar tiller. Secondary tillers form from axillary buds in primary tiller nodes. Not in scale. (Drawn by H. Bäckström).

The development of a tiller can be divided into two different phases: bud formation and bud outgrowth, which both in turn have other interrelated processes (Kerbom et al. 2013, Leduc et al. 2014). Different aspects control these phases: bud formation is mainly directed genetically, but bud outgrowth is affected by genetics, plant hormones and environmental factors, such as light intensity and photoperiod, as well as the interactions of all these factors (Kerbom et al. 2013, Leduc et al. 2014). Hormonal regulation of tillering is not well known, but main factors that are suggested by research are cytokinins, auxins and strigolactones (Kerbom et al. 2013). Cytokinins stimulate the outgrowth of the bud, auxins and strigolactones, in turn, inhibit the bud outgrowth (Leduc et al. 2014).

The emergence of the first main culm tillers is in synchrony with the appearance of the tip of the third and fourth leaf, and so on, on the main culm (Hay and Kirby 1991). The coleoptile tiller emergence is in synchrony with the appearance of the second or third main culm leaf (Rebetzke et al. 2008). This synchrony is essential so that all the grain yielding ears, both main culm and tiller ears, mature at the same time (Hay and Kirby 1991).

Plants with the uniculm growth habit produce only one main culm without tillers (Dofing 1996). Dofing and Karlsson (1993) compared the development of uniculm and conventional tillering barley accessions in the field conditions. According to Dofing and Karlsson (1993), the uniculm barley plants had a greater leaf appearance rate than the conventional tillering ones. The uniculm barley plants also produced more leaves per main culm than the conventional tillering barley plants (Dofing and Karlsson 1993). Dofing and Karlsson (1993) also concluded that the overall development of the uniculm plants required fewer growing degree days than the conventional tillering plants. According to Dofing and Karlsson (1993), the uniculm plants grew taller than the conventional tillering counterparts. However, in later experiments, there were no differences in plant height among the uniculm and the conventional tillering barley accessions (Dofing 1996, Mäkelä and Muurinen 2012).

2.3.2 Number of tillers

Aspinall and Paleg (1964) found that decreasing light intensity (73–292 µmol m^{-2} s^{-1}) or daylength (10 h or 16 h) reduced the number of tillers barley plants produced. Cannell (1969b) showed similarly that low light intensity (146 µmol m^{-2} s^{-1}) reduced the number of tillers. High temperature (24/15 °C day/night) also reduced the number of tillers and a short photoperiod (12.5 h) delayed the tiller appearance (Cannell 1969b). Friend (1965) found that increase in light intensity (from 29.2 and 73 µmol m^{-2} s^{-1} to 255.5 and 365 µmol m^{-2} s^{-1}) increased the rate of wheat tillering. According to Friend et al. (1967), the number of tillers on wheat plants after four weeks of growth increased as the daylength increased (from 8 h to 24 h). However, Miralles and Richards (2000) observed that the long photoperiod (19 h) decreased the number of tillers in wheat and barley when compared to the short photoperiods (9 h and 13 h).

Along with photoperiod, there are also other factors affecting tillering in spring barley and wheat. Kirby and Faris (1972) noticed that plant density affects the tillering in barley as high plant density decreased the number of tillers. According to Simmons et al. (1982), management practices, such as row spacing and seeding rate, affected the tillering in barley. Davidson and Chevalier (1990) observed that water deficiency and plant density affected the number of tillers on wheat. Many of these factors are related to the prevailing light conditions within the crop population. Davis and Simmons (1994) discovered that differences in light quality in the canopy affected barley tillering. Altering light quality and reduction in red:far red ratio supressed the tiller production (Davis and Simmons 1994). Evers et al. (2006) found that red:far red ratio affected the cessation of tillering in wheat. The level of light intercepted by the canopy and the red:far red ratio supressed the bud outgrowth (Evers et al. 2006). Mosaad et al. (1995) reported that water deficiency limited the number of forming tillers on wheat or prevented it completely. Prystupa et al. (2003) investigated the effects of nitrogen and phosphorus fertilization on barley tillering. Nutrient deficiency delayed the start of tillering and modified the duration of tillering (Prystupa et al. 2003).

2.4 Row-type in barley

2.4.1 Ear structure in barley

Cultivated barley has been generally classified into two major groups based on the ear row-type: two-row and six-row barleys (Bonnett 1966). The debate on the origin of the cultivated barley, and whether the wild barley has been a two- or six-rowed plant, has been going on for some time (Tanno et al. 2002). According to Tanno et al. (2002), it is now widely believed that the original wild barley has been two-rowed since its extant form and modern-day relatives are two-rowed and genes resulting in two-rowed phenotype are dominant.

Barley spike consists of alternate and sessile spikelets upon a rachis (Bonnett 1966). Each node of rachis has three single-flowered spikelets from which some are fertile and some sterile (Figure 3) (Bonnett 1966). In the two-row barley only the central spikelet is fertile

and the lateral spikelets are sterile (Bonnett 1966). In the six-row barley all the spikelets are fertile (Bonnett 1966).

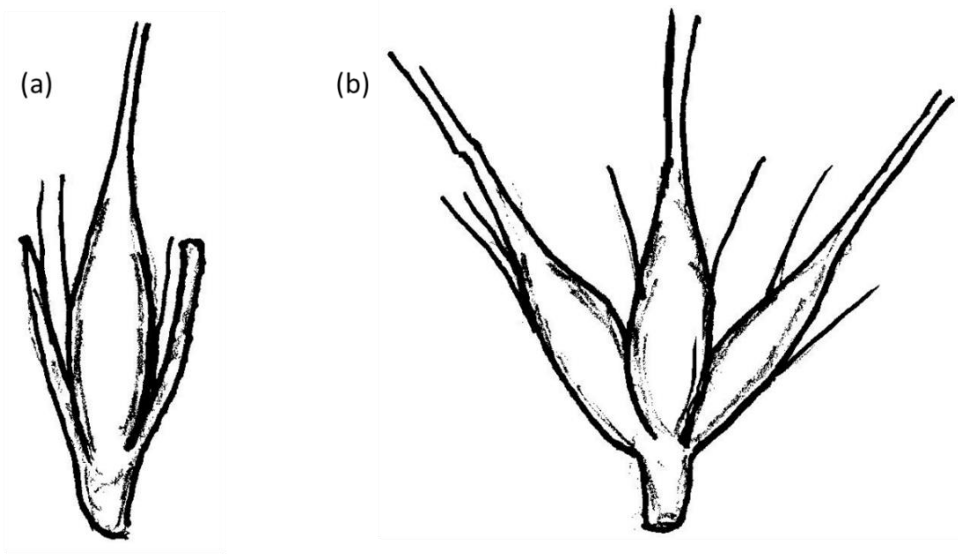

Figure 3. Spikelets of (a) two-row and (b) six-row barley. Not in scale. (Drawn by H. Bäckström).

2.4.2 Differences in row-type traits

Kirby and Riggs (1978) reported that the two-rowed barley produced more leaves per main culm than the six-rowed barley. Kirby and Riggs (1978) also noticed that the main culm leaves of the two-rowed barley emerged faster than the leaves of the six-rowed barley.

Alqudah and Schnurbusch (2015) observed that the leaf growth rate was higher in the six-rowed barley than in the two-rowed barley. Alqudah and Schnurbusch (2015) did not find any differences in the main culm leaf number between the two- and six-rowed barley, but the leaf area in the main culm was greater in the six-rowed barley than in the two-rowed barley. The plant height did not differ between the two row-types (Alqudah et al. 2016).

Alqudah et al. (2016) found that the two-rowed barley produced more tillers per plant than the six-rowed barley. These results are in line with the previous findings of Kirby

and Riggs (1978), who also noticed that the tillering period was longer for the two-rowed barley than for the six-rowed barley. Similar findings regarding the number of tillers were also obtained by Peltonen-Sainio et al. (2009) on field trials where the two-rowed barley produced more tillers than the six-rowed barley and other spring cereals.

2.5 Genetic background

2.5.1 Photoperiod response genes in wheat and barley

Keim et al. (1973) discovered that the photoperiod insensitivity in wheat was linked to two major genes: photoperiod1 (*PPD1*) and photoperiod2 (*PPD2*). Pirasteh and Welsh (1975) found that *PPD1* is in the chromosome 2DS, but the locations of genes *PPD2* and photoperiod3 (*PPD3*) could not be located. Law et al. (1978) located the *PPD3* from the chromosome 2AS and Scarth and Law (1983) the *PPD2* from the chromosome 2BS. Genes *PPD1*, *PPD2* and *PPD3* cause photoperiod insensitivity in wheat accessions (Keim et al. 1973, Pirasteh and Welsh 1975, Law et al. 1978).

Laurie et al. (1994) found photoperiod-H1 gene (*PPD-H1*) in barley. The *PPD-H1* is in the barley chromosome 2(2H) (Laurie et al. 1994). Further investigations on barley genome revealed another daylength related gene, photoperiod-H2 gene (*PPD-H2*), which is located on the chromosome 5(1H) (Laurie et al. 1995). Gene *PPD-H1* affects the flowering time of barley in the long day and *PPD-H2* promotes flowering in the short day (Figure 4) (Laurie et al. 1994, Laurie et al. 1995, Comadran et al. 2012). Digel et al. (2016) reported that, among photoperiod responses, the *PPD-H1* also affects the leaf size of barley.

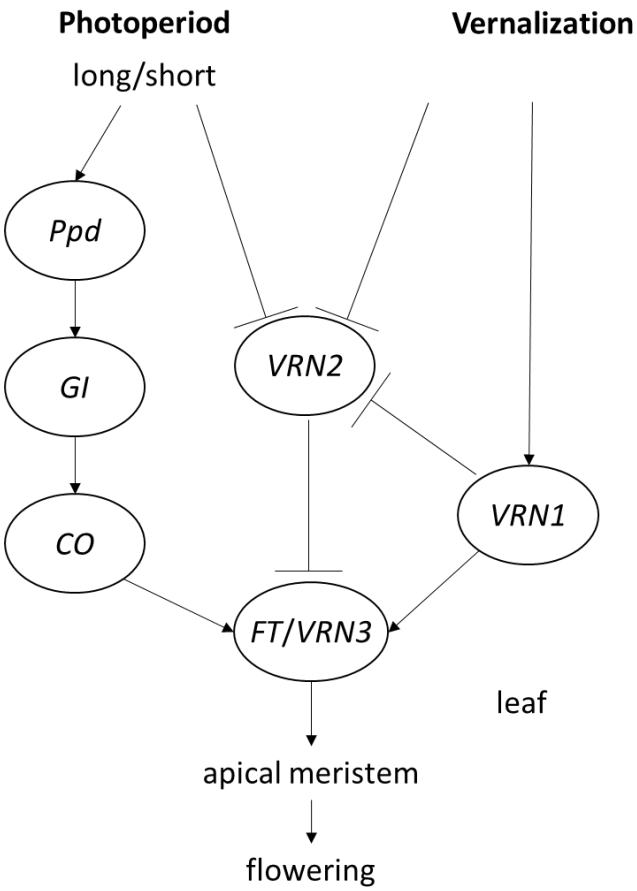

Figure 4. Generalized flowering pathway from leaf to apical meristem in wheat and barley. Arrows indicate promotive interactions and T-bars inhibiting interactions. Adapted from Cocram et al. 2007, Shimara et al. 2009, Deng et al. 2015.

2.5.2 Genes affecting tillering in wheat and barley

Wheat has multiple genes affecting its tillering habits, mainly reducing the number of tillers (Zhang et al. 2012). Spielmeyer and Richards (2004) located a mutant wheat tiller inhibition (*tin1*) gene in the wheat chromosome 1AS. Another wheat tiller inhibition (*TIN2*) gene is in the chromosome 2A (Zhang et al. 2012). According to Kuraparthy et al. (2006), diploid einkorn wheat (*Triticum monococcum* L. subsp. *monococcum*) with mutant tiller inhibition (*tin3*) gene develops only a main culm without tillers, unlike the wild-type diploid einkorn wheat (*T. monococcum* L. subsp. *aegilopoides* (Link) Thell.). Zhang et al. (2012) discovered a mutant fertile tiller inhibition (*ftin*) gene which affects the tiller outgrowth instead of the tiller initiation, like the *TIN1* gene. Like the mutant *tin1*, the *ftin* is in the wheat chromosome 1AS (Zhang et al. 2012).

There are several single genes affecting barley tillering habits and those genes can be divided into two different classes: tiller development promoters and repressors (Babb and Muehlbauer 2003, Dabbert et al. 2009). One of the tiller development promoters is uniculm2 (*CUL2*) which is in the barley chromosome 6(6H) (Babb and Muehlbauer 2003, Dabbert et al. 2009). The *CUL2* mutant (*cul2*) prevents the formation of tillers (Babb and Muehlbauer 2003, Dabbert et al. 2009). Babb and Muehlbauer (2003) observed that *CUL2* is also linked to the development of reproductive shoot apical meristem. Barley lines with mutant absent lower laterals (*als*) produce fewer tillers than the wild-type (Dabbert et al. 2009). Mutant *als* also causes changes in the development of inflorescence (Dabbert et al. 2009). The uniculm gene uc_2 also affects the tillering in barley by producing a uniculm phenotype (Dofing 1996).

Another gene affecting barley tillering habit is the low number of tillers1 (*LNT1*), a mutant (*lnt1*) of which results in barley producing only a few tillers (one to four) and no secondary tillers at all (Dabbert et al. 2010). Tavakol et al. (2015) studied the effects of mutant uniculme4 (*cul4*) gene on the tillering habits and the leaf development of barley. Tavakol et al. (2015) discovered that the mutant *cul4* decreased the number of tillers produced by barley and affected the leaf development. Dabbert et al. (2009) listed various other mutant genes affecting the tillering habits e.g. intermedium spike-b (*int-b*), semi brachytic (*uzu*), densonidosum6 (*den6*), granuma (*gra-a*), intermedium spike-m (*int-m*) and many moded dwarf1 (*mnd1*).

2.5.3 Genes resulting in different row-types in barley

The main gene affecting the row-type in barley is the six-rowed spike1 (*VRS1*), which mutant form *vrs1* results in six-rowed phenotype (Tanno et al. 2002, Koppulu et al. 2013). The *VRS1* is in chromosome 2H (Tanno et al. 2002). According to Koppulu et al. (2013), barley row-type is also controlled by several other loci of *VRS* i.e. *VRS2*, *VRS3*, *VRS4* and intermedium-c (*INT-C*). Rest of the loci *VRS* affect the lateral spikelet fertility in varying degrees and mutant *vrs4* has complete fertility (Koppolu et al. 2013). *VRS2*, *VRS3* and *VRS4* are located on the chromosomes 5HL, 1HL and 3HL respectively (Pourkheirandish and Komatsuda 2007). The intermedium-c locus in the chromosome 4HL described by Lundqvist and Lundqvist (1987) can enhance the effect of *VRS1* (then known as *HEX-V*). Lundqvist and Lundqvist (1987) also noted other intermedium loci (*INT*) having similar

effects on *HEX-V* although varying in competence. Different combinations of independent *vrs* and *int* genes provide diverse set of six-rowed phenotypes (Ramsay et al. 2011). Among row-type determination, the *VRS1* is also considered to contribute to leaf blade area (Thirulogachandar et al. 2017). Thirulogachandar et al. (2017) noted that functional *VRS1* allelle has a negative impact on the leaf width, resulting in narrower leaves and thus in smaller leaf blade area.

3 RESEARCH OBJECTIVES

The aim of this work was to investigate the effects that different photoperiods have on barley leaf and tiller growth. The hypothesis was that the long photoperiod reduces the individual leaf size, main culm leaf area and the number of tillers. Other aims were to compare the effects of uniculm growth habit to conventional tillering growth habit on leaf growth and to compare the differences expressed by the two row-types on leaf and tiller growth. The hypothesis was that the uniculm growth habit results in larger leaf size and leaf area. Other hypothesis was that two-rowed barley accessions have smaller leaves and leaf area but higher tiller number and faster growth rate than the six-rowed accessions.

4 MATERIALS AND METHODS

4.1 Experimental design and plant material

Two experiments were conducted in growth chambers (Weiss Bio 2000, Weiss Technik GmbH (Schunk Group), Heuchelheim, Germany) in the University of Helsinki. The plant material used included seven different spring barley accessions with three pairs of near-isogenic accessions ‘Morex’ and ‘Uniculm Morex’, ‘Kindred’ and ‘Uniculm Kindred’, ‘Ingrid’ and ‘3-503’ and ‘Saana’ (Table 1). The near-isogenic accessions differed in their tillering habit (Dofing 1996). The experiments were organised in a completely randomized design with four replicates, 28 pots per treatment, totalling in 84 pots.

Ten seeds were sown in 3,5 litre plastic pots filled with mixture of pre-fertilised peat (Kekkilä B2 peat (N-P-K:11-4-21), Kekkilä Oyj, Finland) and sand in a ratio of 10:1, respectively. After emergence, the plants were thinned to five per pot. The plants were watered daily. Liquid fertilizer (0.2% Kemiran täyslannos (N-P-K:14-5-21), Kemira Grow-How Oyj, Finland) was applied four times during watering. First fertilizer (0.2% SuperX4 (N-P-K:17-5-25) Kekkilä Oyj, Finland) pot application of 250 ml was at the 4-leaf-stage, and the others 300 ml per pot, every second week.

Table 1. Seven barley accessions used in the experiments.

Accession	Tillering habit	Row-type	Obtained from
Morex	conventional	6	Dr S. Dofing, University of Washington, USA
Uniculm Morex	uniculm	6	Dr S. Dofing, University of Washington, USA
Kindred	conventional	6	Dr S. Dofing, University of Washington, USA
Uniculm Kindred	uniculm	6	Dr S. Dofing, University of Washington, USA
Ingrid	conventional	2	Nordic Gene Bank, Alnarp, Sweden
3-503	uniculm	2	Nordic Gene Bank, Alnarp, Sweden
Saana	conventional	2	Boreal Kasvinjalostus Oy, Finland

4.2 Growing conditions

Photoperiods used in the experiments were 15 h, 18 h and 21 h with a photon flux density (PFD) of 400 µmol m^{-2} s^{-1}. There was a period of dim light for half an hour before each sun rise and sun set. The humidity was between 60/70 % and temperature during the day/night was 18/12 ºC.

4.3 Measurements

The number of leaves and tillers were monitored daily. Leaf length and width was measured after each leaf was full-grown. After the plants had reached the 4-leaf-stage,

one plant from each pot was cut from the soil level for sampling. Following samples were taken as the plants reached subsequent leaf-stages. Each sample was divided into main stem and primary and secondary tillers. The leaf area of an individual fully-grown leaf was calculated by using the formula (1) described by Repková et al. (2009).

$$A = l \times w \times k, \quad (1)$$

where
l = leaf length (mm)
w = leaf width (mm)
k = multiplying factor (0.64)

4.3 Statistical analyses

The analysis of variance (ANOVA) was performed by using SPSS (versions 24.0 and 25.0, IBM Inc., Armonk, NY, USA; replicates as random factors and photoperiod and accession as fixed factors). The multiple comparisons of means were calculated using Tukey's test. The independent sample t-tests were used in comparison of means in row-type and growth habit tests. Pearson correlation was used to analyze the relationships between the number of tillers and the main culm leaf area and the number of tillers per plant and the main culm leaf number. In the calculations on the number of tillers per plant only data from the second experiment was used.

5 RESULTS

5.1 Plant growth under three different photoperiods

The plant growth hastened as the length of the photoperiod increased (Table 2). The time needed to reach the flag-leaf-stage varied depending on the photoperiod, the accession, and their interaction. The time needed varied from 53 to 80 days in the 15 h photoperiod, from 49 to 55 days in the 18 h photoperiod, and from 41 to 49 days in the 21 h photoperiod. 'Saana' was the first to reach the flag-leaf-stage in the 15 h and 18 h

photoperiods. ‘Uniculm Morex’ and ‘Uniculm Kindred’ were the first to reach the flag-leaf-stage in the 21 h photoperiod. In all the studied photoperiods, ‘Ingrid’ was the last to reach the flag-leaf-stage. In the 15 h photoperiod, ‘3-503’ reached the flag-leaf-stage earlier than ‘Ingrid’, but ‘Morex’ and ‘Kindred’ reached the flag-leaf-stage earlier than their uniculm counterparts ‘Uniculm Morex’ and ‘Uniculm Kindred’. Under the longer 18 h and 21 h photoperiods, the uniculm accessions ‘Uniculm Morex’, ‘Uniculm Kindred’ and ‘3-503’ reached the flag-leaf-stage earlier than their conventional tillering counterparts ‘Morex’, ‘Kindred’ and ‘Ingrid’.

Table 2. The number of days required from sowing to flag-leaf stage by the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h). Data shown are means (n = 7–8).

Photoperiod, (h)	Accession	Days from sowing to flag-leaf stage
15	Morex	63
	Uniculm Morex	68
	Kindred	64
	Uniculm Kindred	71
	Ingrid	80
	3-503	78
	Saana	53
18	Morex	54
	Uniculm Morex	49
	Kindred	52
	Uniculm Kindred	49
	Ingrid	55
	3-503	54
	Saana	47
21	Morex	45
	Uniculm Morex	41
	Kindred	45
	Uniculm Kindred	41
	Ingrid	49
	3-503	46
	Saana	43
S.E.M.		54.0
p-value (< 0.05)	Photoperiod (P)	0.000
	Accession (A)	0.000
	P × A	0.000

5.2 Leaf growth under three different photoperiods

5.2.1 Leaf emergence rate

The leaf emergence rate increased as the length of the photoperiod increased. In the first experiment, the photoperiod and the accession affected the leaf emergence rates (Table 3). In the second experiment, the photoperiod, the accession, and their interaction affected the leaf emergence rates (Table 4). In both experiments, the leaf emergence rates under all the studied photoperiods differed from each other, and the leaf emergence rate was the slowest in the 15 h photoperiod. 'Uniculm Morex' had the fastest leaf emergence rates of all the studied accessions. In both experiments, the leaf emergence rate was faster in the uniculm accessions than in the conventional tillering accessions. No differences in the leaf emergence rates between the two row-types were observed.

Table 3. The leaf emergence rate of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Leaf emergence rate
Photoperiod, (h)	15	0.10^{a}
	18	0.12^{b}
	21	0.15^{c}
	S.E.M.	0.001
	p-value	0.000
Accession	Morex	0.13^{a}
	Uniculm Morex	0.13^{a}
	Kindred	0.12^{a}
	Uniculm Kindred	0.12^{a}
	Ingrid	0.12^{a}
	3-503	0.12^{a}
	Saana	0.12^{a}
	S.E.M.	0.001
	p-value	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

Table 4. The leaf emergence rate of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Leaf emergence rate
15	Morex	0.10[a]
	Uniculm Morex	0.11[a]
	Kindred	0.10[a]
	Uniculm Kindred	0.10[a]
	Ingrid	0.11[a]
	3-503	0.11[a]
	Saana	0.10[a]
18	Morex	0.11[a]
	Uniculm Morex	0.12[a]
	Kindred	0.11[a]
	Uniculm Kindred	0.11[a]
	Ingrid	0.11[a]
	3-503	0.11[a]
	Saana	0.11[a]
21	Morex	0.12[ab]
	Uniculm Morex	0.13[b]
	Kindred	0.11[a]
	Uniculm Kindred	0.12[ab]
	Ingrid	0.12[ab]
	3-503	0.13[b]
	Saana	0.11[a]
S.E.M.		0.001
p-value (< 0.05)	Photoperiod (P)	0.000
	Accession (A)	0.000
	P × A	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

5.2.2 Leaf length

The leaf length decreased as the length of the photoperiod increased. In both experiments, the photoperiod and the accession affected the leaf length (Table 5 and 6). Only in the first experiment, the interaction of photoperiod and accession affected the leaf length. In both experiments, the leaves of the studied accessions grown under the 15 h and 18 h photoperiods were longer than the leaves of studied accessions grown under the longest, 21 h photoperiod. In both experiments, ‘Uniculm Kindred’ had the longest leaves in all the studied photoperiods. In the first experiment, ‘Ingrid’ had the shortest leaves in the

15 h and 21 h photoperiods and ‘Saana’ in the 18 h photoperiod. In the second experiment, ‘Saana’ had the shortest leaves in all the studied photoperiods. In both experiments, the two-rowed accessions had shorter leaves than the six-rowed accessions, and the leaves of the conventional tillering accessions were shorter than the leaves of the uniculm accessions.

Table 5. The leaf length of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Leaf length
15	Morex	253^{b}
	Uniculm Morex	279^{bc}
	Kindred	274^{bc}
	Uniculm Kindred	297^{c}
	Ingrid	202^{a}
	3-503	297^{c}
	Saana	203^{a}
18	Morex	252^{ab}
	Uniculm Morex	290^{c}
	Kindred	279^{bc}
	Uniculm Kindred	291^{c}
	Ingrid	225^{a}
	3-503	264^{bc}
	Saana	223^{a}
21	Morex	248^{bc}
	Uniculm Morex	253^{cd}
	Kindred	256^{cd}
	Uniculm Kindred	281^{d}
	Ingrid	211^{a}
	3-503	254^{cd}
	Saana	221^{ab}
S.E.M.		0.1
p-value (< 0.05)	Photoperiod (P)	0.05
	Accession (A)	0.000
	P × A	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

Table 6. The leaf length of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Leaf length
Photoperiod, (h)	15	256[b]
	18	254[b]
	21	245[a]
	S.E.M.	1.6
	p-value	0.01
Accession	Morex	240[b]
	Uniculm Morex	259[c]
	Kindred	267[c]
	Uniculm Kindred	287[d]
	Ingrid	221[a]
	3-503	253[bc]
	Saana	219[a]
	S.E.M.	1.6
	p-value	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

5.2.3 Leaf width and leaf length/width ratio

The leaf width decreased as the length of the photoperiod increased. In both experiments, the photoperiod, the accession, and their interaction affected the leaf width (Table 7). In both experiments, the leaf widths of the studied accessions grown under the 15 h and 18 h photoperiods did not differ from each other. Leaves of accessions grown under the longest, 21 h photoperiod, were narrower than the leaves of the accessions grown under the two other studied photoperiods. In both experiments, ‘Uniculm Kindred’ had the widest leaves in all the studied photoperiods. On the other hand, in both experiments, ‘Ingrid’ had the narrowest leaves in all the studied photoperiods. In both experiments, the two-rowed accessions had narrower leaves than the six-rowed accessions, and the uniculm accessions had wider leaves than the conventional tillering accessions.

The leaf length/width ratio increased as the length of the photoperiod increased. In both experiments, the leaf length/width ratio was affected by the photoperiod, the accession, and their interaction (Table 7). In the second experiment, under the longest photoperiod (21 h), the leaf length/width ratios of the studied accessions were bigger than the leaf

length/width ratios of the studied accessions grown under the two other photoperiods (15 h and 18 h). In both experiments, '3-503' had the biggest leaf length/width ratios in all the studied photoperiods. In both experiments, the two-rowed accessions had bigger leaf length/width ratios than the six-rowed accessions, and the conventional tillering accessions had smaller leaf length/width ratios than the uniculm accessions.

Table 7. The leaf width and leaf length/width ratio of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h). Data shown are means (n = 4).

		Experiment 1		Experiment 2	
Photoperiod, (h)	Accession	Leaf width	Leaf L/W	Leaf width	Leaf L/W
15	Morex	13^{cd}	20^{b}	13^{b}	19^{a}
	Uniculm Morex	15^{e}	19^{ab}	13^{bc}	19^{a}
	Kindred	14^{de}	20^{b}	14^{c}	20^{a}
	Uniculm Kindred	16^{f}	19^{ab}	15^{d}	20^{a}
	Ingrid	10^{a}	21^{b}	10^{a}	24^{b}
	3-503	11^{ab}	27^{c}	10^{a}	25^{b}
	Saana	12^{bc}	17^{a}	10^{a}	21^{a}
18	Morex	13^{c}	19^{a}	13^{c}	20^{a}
	Uniculm Morex	15^{d}	19^{a}	13^{cd}	20^{a}
	Kindred	14^{c}	20^{ab}	14^{d}	21^{a}
	Uniculm Kindred	15^{d}	19^{a}	15^{e}	19^{a}
	Ingrid	10^{a}	23^{b}	9^{a}	23^{b}
	3-503	10^{a}	27^{c}	10^{ab}	26^{c}
	Saana	12^{b}	19^{a}	11^{b}	20^{a}
21	Morex	12^{c}	20^{a}	11^{c}	20^{a}
	Uniculm Morex	13^{c}	20^{a}	11^{c}	22^{ab}
	Kindred	12^{c}	21^{ab}	11^{c}	23^{bc}
	Uniculm Kindred	14^{d}	20^{a}	13^{d}	23^{bc}
	Ingrid	9^{a}	23^{b}	9^{a}	25^{c}
	3-503	10^{ab}	25^{c}	9^{a}	28^{d}
	Saana	10^{b}	21^{ab}	10^{b}	21^{ab}
S.E.M.		0.1	0.1	0.1	0.1
p-value (< 0.05)	Photoperiod (P)	0.000	0.05	0.000	0.000
	Accession (A)	0.000	0.000	0.000	0.000
	P × A	0.000	0.01	0.000	0.01

Mean values with the same letter do not differ significantly at $P < 0.05$

5.2.4 Main culm leaf number at which the leaf reached its maximum length and width

The main culm leaf number at which the maximum leaf length was reached was affected by the accession and the photoperiod × accession interaction in the first experiment (Table 8). In the second experiment, the photoperiod and the accessions affected the main culm leaf number at which the maximum leaf length was reached (Table 9). In the first experiment, the leaf number at which the maximum leaf length was reached earliest was in the shortest, 15 h photoperiod. In the second experiment, in turn, the leaf number at which the maximum leaf length was reached in the latest main culm leaf number was in the shortest, 15 h photoperiod.

In the first experiment, in ‘Morex’ and ‘3-503’ the main culm leaf number at which the maximum leaf length was reached was the same in all the studied photoperiods. ‘3-503’ also had the highest main culm leaf number at which the maximum leaf length was reached. In ‘Uniculm Kindred’ the leaf number at which the maximum leaf length was reached decreased as the length of the photoperiod increased. In ‘Uniculm Morex’ the lowest leaf number at which the maximum leaf length was reached occurred in the 18 h photoperiod. In the other accessions, the main culm leaf number at which the maximum leaf length was reached increased as the length of the photoperiod increased.

In the second experiment, in ‘Morex’ and ‘Ingrid’ the main culm leaf number at which the maximum leaf length was reached was the same in all the studied photoperiods. In ‘Saana’ the maximum leaf length was reached earlier in the 15 h and 21 h photoperiods than in the 18 h photoperiod. In the other accessions, the main culm leaf number at which the maximum leaf length was reached decreased as the length of the photoperiod increased. In the first experiment, the two-rowed accessions reached the maximum leaf length in the later main culm leaf number than the six-rowed accessions. The conventional tillering accessions reached the maximum leaf length in the earlier main culm leaf number than the uniculm accessions in both experiments.

In general, the leaf number at which the maximum leaf width was reached decreased as the length of the photoperiod increased, except in ‘Ingrid’, ‘3-503’ and ‘Saana’ in the first experiment, and ‘Uniculm Kindred’ and ‘Saana’ in the second experiment. The main culm leaf number at which the maximum leaf width was reached was affected by the

photoperiod, the accession, and their interaction in both experiments (Table 10). In ‘Ingrid’ the main culm leaf number at which the maximum leaf width was reached was the lowest in the shortest, 15 h photoperiod. In ‘3-503’ and ‘Uniculm Kindred’ the lowest main culm leaf number at which the maximum leaf width was reached was in the 18 h photoperiod. In both experiments, the main culm leaf number at which the maximum leaf width was reached in ‘Saana’ was the same in all the studied photoperiods. In the first experiment, the two-rowed accessions reached the maximum leaf width in the earlier main culm leaf number than the six-rowed accessions. In the second experiment, the conventional tillering accessions reached the maximum leaf width in the earlier main culm leaf number than the uniculm accessions.

Table 8. The leaf number at which the maximum leaf length was reached in the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Leaf number
15	Morex	5
	Uniculm Morex	7
	Kindred	4
	Uniculm Kindred	7
	Ingrid	5
	3-503	8
	Saana	5
18	Morex	5
	Uniculm Morex	6
	Kindred	5
	Uniculm Kindred	6
	Ingrid	6
	3-503	8
	Saana	6
21	Morex	5
	Uniculm Morex	7
	Kindred	5
	Uniculm Kindred	6
	Ingrid	6
	3-503	8
	Saana	6
S.E.M.		6.0
p-value (< 0.05)	Photoperiod (P)	0.259
	Accession (A)	0.000
	P × A	0.01

Table 9. The main culm leaf number at which the maximum leaf length was reached in the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Leaf number
Photoperiod, (h)	15	7
	18	6
	21	6
	S.E.M.	0.1
	p-value	0.01
Accession	Morex	6
	Uniculm Morex	7
	Kindred	5
	Uniculm Kindred	6
	Ingrid	6
	3-503	8
	Saana	5
	S.E.M.	0.1
	p-value	0.000

Table 10. The main culm leaf number at which the maximum leaf width was reached in the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h). Data shown are means (n = 4).

Photoperiod, (h)	Accession	Experiment 1 Leaf number	Experiment 2 Leaf number
15	Morex	10	10
	Uniculm Morex	9	10
	Kindred	9	9
	Uniculm Kindred	9	10
	Ingrid	6	10
	3-503	10	11
	Saana	7	7
18	Morex	8	9
	Uniculm Morex	8	9
	Kindred	8	8
	Uniculm Kindred	8	8
	Ingrid	7	9
	3-503	3	9
	Saana	7	7
21	Morex	7	9
	Uniculm Morex	8	9
	Kindred	7	8
	Uniculm Kindred	8	9
	Ingrid	7	8
	3-503	9	9
	Saana	7	7
S.E.M.		7.7	8.7
p-value (< 0.05)	Photoperiod (P)	0.01	0.01
	Accession (A)	0.01	0.000
	P × A	0.000	0.05

5.2.5 Final leaf number on the main culm

The final leaf number on the main culm decreased as the length of the photoperiod increased, except in some accessions: ‘Saana’ and ‘Ingrid’, in the first experiment, and ‘Kindred’, ‘3-503’ and ‘Saana’, in the second experiment. In both experiments, the final leaf number on the main culm was affected by the photoperiod, the accession, and their interaction (Table 11).

‘3-503’ had the highest and ‘Ingrid’ the lowest final main culm leaf number in the shortest, 15 h photoperiod. In both experiments, the final main culm leaf number in ‘Saana’ was the same in all the studied photoperiods. In the second experiment, ‘Kindred’ and ‘3-503’ had the lowest final leaf number in the 18 h photoperiod. In the first experiment, the final leaf number was higher in the uniculm accessions than in their conventional tillering counterparts, and the two-rowed accessions had fewer leaves on their main culm than the six-rowed accessions.

Table 11. The final leaf number of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h). Data shown are means (n = 3–4).

		Experiment 1	Experiment 2
Photoperiod, (h)	Accession	Final leaf number	Final leaf number
15	Morex	10	11
	Uniculm Morex	11	12
	Kindred	9	10
	Uniculm Kindred	10	11
	Ingrid	7	12
	3-503	12	14
	Saana	8	8
18	Morex	10	10
	Uniculm Morex	11	11
	Kindred	9	9
	Uniculm Kindred	10	10
	Ingrid	8	10
	3-503	11	11
	Saana	8	8
21	Morex	9	10
	Uniculm Morex	10	11
	Kindred	8	10
	Uniculm Kindred	9	10
	Ingrid	9	10
	3-503	10	12
	Saana	8	8
S.E.M.		0.2	0.2
p-value (< 0.05)	Photoperiod (P)	0.05	0.000
	Accession (A)	0.000	0.000
	P × A	0.000	0.01

5.3 Main culm leaf area under three different photoperiods

The main culm leaf area decreased as the length of the photoperiod increased. In both experiments, the main culm leaf area was affected by the photoperiod, the accession, and their interaction (Table 12). In the first experiment, the main culm leaf area in all the studied photoperiods differed from each other, progressively decreasing as the length of the photoperiod increased. In the second experiment, the smallest main culm leaf area in the longest, 21 h photoperiod, differed from the larger main culm leaf areas in the two other photoperiods.

In both experiments and under all the studied photoperiods, ‘Uniculm Kindred’ had the largest main culm leaf area. On the other hand, in both experiments and under all the studied photoperiods, ‘Ingrid’ had the smallest leaf area. In both experiments, the main culm leaf area was smaller in the two-rowed accessions than in the six-rowed accessions, and the main culm leaf area was larger in the uniculm accessions than in the conventional tillering accessions.

Table 12. The main culm leaf area of the studied seven barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h). Data shown are means (n = 4).

Photoperiod, (h)	Accession	Experiment 1 Leaf area	Experiment 2 Leaf area
15	Morex	2112^{bc}	2053^{bc}
	Uniculm Morex	2767^{d}	2392^{cd}
	Kindred	2518^{cd}	2491^{d}
	Uniculm Kindred	3330^{e}	3095^{e}
	Ingrid	1277^{a}	1433^{a}
	3-503	2160^{bc}	1710^{ab}
	Saana	1689^{ab}	1587^{a}
18	Morex	2222^{b}	2123^{b}
	Uniculm Morex	2974^{c}	2337^{bc}
	Kindred	2545^{b}	2549^{cd}
	Uniculm Kindred	3000^{c}	2870^{d}
	Ingrid	1455^{a}	1392^{a}
	3-503	1674^{a}	1684^{a}
	Saana	1773^{a}	1646^{a}
21	Morex	2006^{cd}	1711^{bc}
	Uniculm Morex	2144^{d}	1970^{c}
	Kindred	2147^{d}	1934^{c}
	Uniculm Kindred	2685^{e}	2484^{d}
	Ingrid	1264^{a}	1204^{a}
	3-503	1675^{bc}	1433^{ab}
	Saana	1539^{ab}	1448^{ab}
S.E.M.		25.3	20.2
p-value (< 0.05)	Photoperiod (P)	0.000	0.000
	Accession (A)	0.000	0.000
	P × A	0.000	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

5.4 Tiller growth under three different photoperiods

5.4.1 Tiller growth and emergence rate

In the first experiment, all the accessions had tillers from TC to T4 under all the studied photoperiods, except ‘Morex’ which did not produce TC tiller in the 18 h photoperiod. In the second experiment, ‘Morex’ and ‘Kindred’ produced tillers from TC to T5 and ‘Saana’ from TC to T4 in the shortest, 15 h photoperiod. ‘Ingrid’ produced tillers from

TC to T6 in the 15 h and 21 h photoperiods and to T5 in the 18 h photoperiod. All the other accessions produced tillers from TC to T4 in the two longer, 18 h and 21 h, photoperiods. In total, majority of the produced tillers were T1 tillers. In both experiments, there were more T2 tillers produced than TC tillers. The total number of produced tillers decreased from T3 to T6.

The tiller emergence rates increased along with longer photoperiod. In the first experiment, the photoperiod and the photoperiod × accession interaction affected the tiller emergence rates (Table 13). In the first experiment, the tiller emergence rates of the studied accessions under the 15 h and 18 h photoperiods did not differ from each other. The tiller emergence rates of the studied accessions grown under the longest, 21 h photoperiod, were faster than the tiller emergence rates of the studied accessions grown under the two other studied photoperiods (15 h and 18 h). In the second experiment, the photoperiod and the accession affected the rate of tiller emergence (Table 14). In the second experiment, all the tiller emergence rates of the studied accessions under the studied photoperiods differed from each other. In the second experiment, the two-rowed accessions had faster tiller emergence rates than the six-rowed accessions.

Table 13. The tiller emergence rate of the studied four conventional tillering barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Tiller emergence rate
15	Morex	0.13[c]
	Kindred	0.12[bc]
	Ingrid	0.07[a]
	Saana	0.09[ab]
18	Morex	0.10[a]
	Kindred	0.10[a]
	Ingrid	0.12[a]
	Saana	0.10[a]
21	Morex	0.16[a]
	Kindred	0.17[a]
	Ingrid	0.18[a]
	Saana	0.18[a]
S.E.M.		0.004
p-value (< 0.05)	Photoperiod (P)	0.000
	Accession (A)	0.373
	P × A	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

Table 14. The tiller emergence rate of the studied four conventional tillering barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Tiller emergence rate
Photoperiod, (h)	15	0.11[a]
	18	0.14[b]
	21	0.18[c]
	S.E.M	0.003
	p-value	0.000
Accession	Morex	0.12[a]
	Kindred	0.13[ab]
	Ingrid	0.15[b]
	Saana	0.15[b]
	S.E.M	0.003
	p-value	0.01

Mean values with the same letter do not differ significantly at $P < 0.05$

5.4.2 Number of tillers

The number of tillers increased along with the longer photoperiod, except for ‘Morex’ and ‘Kindred’ in the first experiment. In the first experiment, the photoperiod and the photoperiod × accession interaction affected the number of tillers (Table 15). The photoperiod and the accession affected the number of tillers in the second experiment (Table 16). In both experiments, the number of tillers in all the studied accessions grown under the 15 h and 18 h photoperiods did not differ from each other. The number of tillers of the studied accessions grown under the longest, 21 h photoperiod, were higher than the number of tillers of the studied accessions grown under the two other studied photoperiods. In the second experiment, ‘Ingrid’ was the only accession that differed from the other studied accessions. In the second experiment, the two-rowed accessions produced more tillers than the six-rowed accessions.

Table 15. The number of tillers in the studied four conventional tillering barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Number of tillers
15	Morex	4.8^{b}
	Kindred	4.6^{b}
	Ingrid	3.0^{a}
	Saana	3.5^{ab}
18	Morex	4.6^{a}
	Kindred	3.8^{a}
	Ingrid	4.3^{a}
	Saana	3.7^{a}
21	Morex	4.5^{a}
	Kindred	4.7^{a}
	Ingrid	4.7^{a}
	Saana	4.9^{a}
S.E.M.		0.09
p-value (< 0.05)	Photoperiod (P)	0.01
	Accession (A)	0.117
	P × A	0.01

Mean values with the same letter do not differ significantly at $P < 0.05$

Table 16. The number of tillers in the studied four conventional tillering barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Number of tillers
Photoperiod, (h)	15	4.2[a]
	18	4.6[a]
	21	5.1[b]
	S.E.M.	0.07
	p-value (< 0.05)	0.01
Accession	Morex	4.0[a]
	Kindred	4.1[a]
	Ingrid	5.4[b]
	Saana	4.3[a]
	S.E.M.	2.76
	p-value (< 0.05)	0.000

Mean values with the same letter do not differ significantly at $P < 0.05$

The number of tillers correlated positively with the main culm leaf area in both experiments (Table 17).

Table 17. Pearson correlation coefficients between number of tillers and main culm leaf area ($n = 177$ for experiment 1; $n = 359$ for experiment 2).

	Number of tillers	
	Exp 1	Exp 2
Leaf area	0.188*	0.218**

*, ** $P < 0.05$, 0.01, respectively

5.4.3 Number of tillers per plant

The number of tillers per plant was affected by the accession and the photoperiod × accession interaction (Table 18). ‘Ingrid’ had more tillers per plant than the other studied accessions. The two-rowed accessions had more tillers per plant than the six-rowed accessions. The number of tillers per plant also correlated positively with the main culm

leaf number (r = 0.407, n = 1388, $P < 0.01$). Only the data from the second experiment were used in number of tillers per plants calculations.

Table 18. The number of tillers per plant in the studied four conventional tillering barley accessions when grown under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Tillers per plant
15	Morex	1.5^{b}
	Kindred	1.2^{ab}
	Ingrid	2.2^{c}
	Saana	1.1^{a}
18	Morex	1.6^{a}
	Kindred	1.4^{a}
	Ingrid	2.0^{b}
	Saana	1.3^{a}
21	Morex	1.3^{a}
	Kindred	1.4^{a}
	Ingrid	2.3^{b}
	Saana	1.4^{a}
S.E.M.		0.03
p-value (< 0.05)	Photoperiod (P)	0.246
	Accession (A)	0.000
	P × A	0.01

Mean values with the same letter do not differ significantly at $P < 0.05$

5.4.4 Maximum number of tillers

The maximum number of tillers was affected by the photoperiod and the photoperiod × accession interaction (Table 19) in the first experiment, but only by the accession in the second experiment (Table 20). In the first experiment, ‘Morex’ and ‘Kindred’ produced the maximum number of tillers in the shortest, 15 h photoperiod, ‘Ingrid’ and ‘Saana’ in the 18 h photoperiod. In the longest, 21 h photoperiod, ‘Morex’ and ‘Ingrid’ produced the maximum number of tillers. In the second experiment, ‘Ingrid’ produced the maximum number of tillers in all the studied photoperiods. The two-rowed accessions had higher maximum number of tillers than the six-rowed accessions in the second experiment.

The occurrence of maximum number of tillers was affected by the photoperiod and the photoperiod × accession interaction in the first experiment (Table 21), but only by the accession in the second experiment (Table 22). The maximum number of tillers occurred in the earliest date under the longest, 21 h photoperiod. In the second experiment, the six-rowed accessions reached the maximum tiller number earlier than the two-rowed accessions.

Table 19. The maximum number of tillers in the four conventional tillering barley accessions under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Maximum number of tillers
15	Morex	9
	Kindred	9
	Ingrid	6
	Saana	6
18	Morex	9
	Kindred	8
	Ingrid	10
	Saana	9
21	Morex	11
	Kindred	9
	Ingrid	11
	Saana	10
S.E.M.		0.3
p-value (< 0.05)	Photoperiod (P)	0.01
	Accession (A)	0.377
	P × A	0.01

Table 20. The maximum number of tillers in the four conventional tillering barley accessions under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Maximum number of tillers
Photoperiod, (h)	15	10
	18	10
	21	11
	S.E.M.	0.4
	p-value	0.160
Accession	Morex	9
	Kindred	9
	Ingrid	14
	Saana	9
	S.E.M.	0.4
	p-value	0.000

Table 21. Days from sowing at which the maximum number of tillers occurred in the four conventional tillering barley accessions under three different photoperiods (15 h, 18 h and 21 h) in the first experiment. Data shown are means (n = 4).

Photoperiod, (h)	Accession	Days from sowing
15	Morex	35
	Kindred	31
	Ingrid	33
	Saana	38
18	Morex	38
	Kindred	38
	Ingrid	45
	Saana	38
21	Morex	21
	Kindred	23
	Ingrid	21
	Saana	21
S.E.M.		1.2
p-value (< 0.05)	Photoperiod (P)	0.000
	Accession (A)	0.08
	P × A	0.05

Table 22. Days from sowing at which the maximum number of tillers occurred in the four conventional tillering barley accessions under three different photoperiods (15 h, 18 h and 21 h) in the second experiment. Data shown are means of 4 replicates calculated over either photoperiods or accession.

Treatment		Days from sowing
Photoperiod, (h)	15	30
	18	33
	21	33
	S.E.M.	1.3
	p-value	0.584
Accession	Morex	27
	Kindred	31
	Ingrid	41
	Saana	29
	S.E.M.	1.3
	p-value	0.01

6 DISCUSSION

6.1 Differences on leaf and plant growth under three different photoperiods

As the length of the photoperiod increased, the barley leaves became shorter and narrower. Similar results were obtained by Pararajasingham and Hunt (1996) who investigated the effects of photoperiod on the leaves of spring wheat accessions. However, the shortest and narrowest leaves were observed in the shortest, 8 h photoperiod (Pararajasingham and Hunt 1996). Digel et al. (2016) concluded that photoperiod response effects associated with *Ppd-H1* gene also affect the leaf size on spring barley. Under the long, 16 h photoperiod, the leaves were longer than in the short, 8 h photoperiod (Digel et al. 2016).

The effect of photoperiod on barley leaf width is less studied than the effect of photoperiod on barley leaf length. Aspinall and Paleg (1964) observed that both the photoperiod and the light intensity affected the barley leaf width. Main culm leaves from the first to the third were narrower under the long, 16 h photoperiod, and the high light

intensity (292 µmol m^{-2} s^{-1}) but wider after the fourth main culm leaf (Aspinall and Paleg 1964). In the short, 10 h photoperiod, or in the lower light intensities (73–145 µmol m^{-2} s^{-1}) the leaves were narrower than in the long, 16 h photoperiod (Aspinall and Paleg 1964). However, in this study the light intensity used was higher than in the study of Aspinall and Paleg (1964).

The two-rowed accessions, all originating from the Nordic countries, had shorter and narrower leaves than the six-rowed accessions from North America and Central Europe. Thirulogachandar et al. (2017) obtained similar results on leaf widths of the two-rowed accessions. The leaves of the two-rowed barley were narrower than the leaves of the six-rowed accessions, but the leaf length was not affected by the row-type (Thirulogachandar et al. 2017). In uniculm accessions the leaves were longer and wider than the leaves of the conventional tillering accessions. Similar results have been previously obtained with two- and six-rowed uniculm accessions. Kirby (1973) observed that the two-rowed barley 'uniculm Proctor' had longer leaves and the mature leaves were generally heavier than its tillering counterpart 'Proctor'. Furthermore, Balkema-Boomstra and Mastebroek (1993) observed that the six-rowed barley uniculm lines had leaves that were lax and medium in length compared to the tillering barley lines.

The final leaf number on the main culm decreased as the length of the photoperiod increased. These findings are in accordance with the results obtained earlier on wheat and barley (Pararajasingham and Hunt 1996, Miralles and Richards 2000). In the first experiment, the two-rowed accessions had lower final leaf number on the main culm than the six-rowed accessions. In the second experiment, no differences in final main culm leaf number were observed between the two row-types. This result differs from the previous findings of Kirby and Riggs (1978) that the two-rowed accessions produced more leaves on the main culm than the six-rowed accessions. However, Alqudah and Schnurbusch (2015) did not find such differences between the two row-types. In the first experiment, the uniculm accession had more main culm leaves than the conventional tillering accessions. Similar results have been obtained previously on uniculm barley (Dofing and Karlsson 1993). However, in the second experiment such differences were not observed.

The size of individual leaves and the final leaf number on the main culm contribute to the final main culm leaf area. As on the independent leaf size and on the final main culm leaf number, similarly, the main culm leaf area decreased as the length of the photoperiod increased in this study. These results support the findings from the previous ones on wheat (Williams and Williams 1965) but contradict the findings obtained by Friend et al. (1967). Aspinall and Paleg (1964) observed that rather than daylength, the light intensity affected the barley leaf area. In the short, 10 h photoperiod, the leaf area was smaller than in the long, 16 h photoperiod (Aspinall and Paleg 1964). The main culm leaf area varied between the accessions used in this study, but the two-rowed accessions had smaller leaf area compared to the six-rowed accessions, which is partly explained by the generally smaller individual leaf size in the two-rowed accessions. For similar reasons, the main culm leaf area was smaller in the conventional tillering accessions than in the uniculm accessions.

The main culm leaf number at which the maximum leaf length and width were observed varied between the studied photoperiods and accessions. The main culm leaf number at which the maximum leaf length was reached occurred at the later main culm leaf number as the length of the photoperiod increased in the first experiment. However, in the second experiment the maximum leaf length was reached at the earlier main culm leaf number as the length of the photoperiod increased. Pararajasingham and Hunt (1996) discovered that the effects of increased photoperiod on the wheat leaf length were visible in an earlier leaf number as the daylength increased. Field experiments conducted on wheat supported the earlier findings of the daylength effects on the leaf size (Hotsonyame and Hunt 1998). Digel et al. (2016) observed that the maximum barley leaf length was reached at an earlier main culm leaf number under the long, 16 h photoperiod, than under the short, 8 h photoperiod. The main culm leaf number at which the maximum leaf width was observed decreased as the length of the photoperiod increased. The effect of photoperiod on the occurrence of the maximum leaf width on barley and wheat seems to be less investigated. Aspinall and Paleg (1964) observed that the occurrence of maximum leaf width was affected by both the photoperiod and the light intensity.

The leaf length/width ratio increased as the length of the photoperiod increased and thus the ratio was the biggest in the longest, 21 h photoperiod studied. Aspinall and Paleg (1964) noticed that under the long, 16 h daylength, the leaf length/width ratio was smaller

than under the short, 10 h daylength, especially under the low light intensity. Aspinall and Paleg (1964) concluded that the light intensity rather than the daylength affected the leaf length/width ratio. Similarly, in this study the high light intensity (400 µmol m^{-2} s^{-1}) may have affected more than the length of the photoperiod. The two-rowed accessions had bigger leaf length/width ratios than the six-rowed accessions. The uniculm accessions as well had bigger ratios than the conventional tillering accessions. Changes in leaf length/width ratio imply changes in leaf shapes generally but other experiments on the leaf length/width ratio on barley and wheat seems to be limited.

The leaf emergence rate was slowest in the shortest, 15 h photoperiod, and faster in the longer 18 h and 21 h photoperiods. The long photoperiod thus hastens the leaf emergence rate and similar results have been obtained previously on wheat and barley (Cao and Moss 1989a, Miralles and Richards 2000). There were no differences observed between the leaf emergence rates of the two row-types in this study. This, however, contradicts with the previous findings of Kirby and Riggs (1978), who observed that the two-rowed accessions had higher leaf emergence rates than the six-rowed accessions. The uniculm accessions had faster leaf emergence rates than the conventional tillering accessions, and similar results have been obtained previously on uniculm barley (Kirby 1973, Dofing and Karlsson 1993).

As with the leaf emergence rates, under the longer 18 h and 21 h photoperiods the plant growth was hastened compared to the shortest, 15 h photoperiod. Similar findings have been obtained previously on barley and wheat (Guitard 1960, Aspinall 1966, Kernich et al. 1996). No differences in growth rates between the two row-types were observed in this study. Kirby and Riggs (1978) concluded that collar, leaf and ear initiation took longer time for two-rowed ‘Proctor’ than six-rowed ‘Clermont’. Similarly, the time needed to reach anthesis was longer for two-rowed ‘Proctor’ than for six-rowed ‘Clermont’ (Kirby and Riggs 1978). The growth rates of uniculm accessions did not differ from the growth rates of conventional tillering accessions in this study, which differs from the earlier findings of Dofing and Karlsson (1993).

6.2 Differences on tiller growth under three different photoperiods

The number of tillers increased as the length of the photoperiod increased, especially in the longest, 21 h photoperiod. Similar results have been obtained earlier by Aspinall and Paleg (1964). The findings of this study differ from the generally accepted view that the long photoperiod inhibits the ear bearing tiller formation on barley and wheat (Fairey et al. 1975, Miralles and Richards 2000, Peltonen-Sainio et al. 2009). In this study, all forming tillers were accounted for whether they bore an ear or not. Also, in this study, the plant density was low, nutrient and water supplies were adequate and light intensity was high. Generally, limitations in these factors and high plant density inhibits the tiller formation (Kirby and Faris 1972, Lauer and Simmons 1989, Prystupa et al. 2003, Evers et al. 2006). The two-rowed accessions produced more tillers than the six-rowed accessions as previously reported in the field experiments conducted in Finland (Peltonen-Sainio et al. 2009).

The number of tillers produced per plant was not affected by the photoperiod, but some of the accessions produced more tillers per plant than others, and the two-rowed accessions had more tillers per plant than the six-rowed accessions. This was expected as it is in line with the previous findings (Peltonen-Sainio et al. 2009). The lack of photoperiod effect on the tiller number per plant was unexpected as increase in the length of the photoperiod generally results in lower number of tillers (Fairey et al. 1975, Miralles and Richards 2000). The number of tillers per plant correlated positively with the main culm leaf number in this study.

The photoperiod affected the tiller emergence rate, which was hastened as the daylength increased. This would be expected as the increase in daylength generally hastens the plant growth. Similar results were obtained by Aspinall and Paleg (1964), who observed that increase in the daylength or in the light intensity increased the tiller emergence rate on barley. Miralles and Richards (2000) compared the tiller formation on wheat and barley in interchanged photoperiods. When wheat and barley plants were moved from 19 h to 13 h daylength, the tiller emergence rate was faster, and similarly slower when moved from the short, 13 h daylength, to the longer, 19 h daylength (Miralles and Richards 2000).

In general, barley had faster tiller emergence rate than wheat (Miralles and Richards 2000). The two-rowed accessions had faster tiller emergence rates than the six-rowed accessions. As the two-rowed accessions had faster tiller emergence rate, more tillers could be produced during the experiments compared to the six-rowed accessions. This is in line with the previous observations on the two-rowed and six-rowed barley (Kirby and Riggs 1978).

Nearly all the studied conventional tillering accessions had tillers from coleoptilar node to the fourth main stem leaf node in the first experiment. In the second experiment, the differences among the accessions were more defined than in the first experiment. In the second experiment, in the shortest, 15 h photoperiod, almost all the conventional tillering accessions had tillers even on the fifth or sixth main culm leaf node. 'Ingrid' had tillers up to the fifth and sixth main culm leaf node in the longer 18 h and 21 h photoperiods, respectively. In the other conventional tillering accessions, the tillers occurred only up to the fourth main culm leaf node in the two longer 18 h and 21 h photoperiods. Cannell (1969a) concluded that barley varieties differ in their tillering pattern and in the occurrence of coleoptile tiller and the first main culm tiller. The late developing tillers in the upper leaf nodes are an especially undesirable trait since those tillers rarely produce mature ears and decrease the yield quality (Cannell 1969a, Peltonen-Sainio et al. 2009).

The coleoptile tillers have a role in the early vigour and adding of ground cover in the early stages of the growing season (Rebetzke et al. 2008). Cannell (1969a) outlined possible explanations for varying coleoptile tiller occurrence between different barley varieties, such as the variety itself, nutrient supply and plant spacing. Rebetzke et al. (2008) identified cool air temperature (15–19 ºC mean maximum temperature) and adequate soil nitrogen levels (soil N and additional 40 kg/ha N), among genotypic characteristics, as important factors in coleoptile tiller formation on wheat. Similar, cool air temperatures (18/12 ºC day/night) were used in this study with adequate nitrogen fertilization, as in the field experiments of Rebetzke et al. (2008).

The maximum number of tillers was affected by the daylength in the first experiment and by the accession in the second experiment. Generally, the two-rowed accession 'Ingrid' had the highest maximum number of tillers, especially in the second experiment. As previously stated, the two-rowed accessions do produce more tillers with faster tiller

emergence rates than the six-rowed accessions (Kirby and Riggs 1978, Peltonen-Sainio et al. 2009). The increase in the length of the photoperiod hastened the occurrence of the maximum number of tillers, as it hastens the plant growth and tiller growth in general (Guitard 1960, Aspinall and Paleg 1964, Aspinall 1966, Kernich et al. 1996). In the second experiment, the six-rowed accessions reached the maximum number of tillers faster than the two-rowed accessions.

The number of tillers positively correlated with the main culm leaf area. Thus the plants had resources to grow both large main culm leaves and tillers to increase the total leaf area. Tillers are often considered to compete with the main culm and to be a wasteful use of resource in cereals (Donald 1968, Kirby and Jones 1977). The tillers have shifting roles from benefactor to competitor of the main culm depending on the developmental stage (Kirby and Faris 1972) and as such act as a compensatory mechanism in plants (Cannell 1969a).

6.3 Effect of uniculm growth habit on barley yield formation

When formatting his ideotype on wheat, Donald (1968) raised the question about the role of tillers in cereals with high harvest index. In the wheat ideotype the lack of tillers was regarded as an advantage in terms of efficient use of resources (Donald 1968). As most of the produced tillers did not survive to maturity and did not contribute to the final grain yield, their necessity was questioned (Donald 1968, Kirby and Jones 1977). The forming tillers competed with the main culm on various resources, such as water and nutrients (Jones and Kirby 1977, Kirby and Jones 1977), although the competition among main culm and tillers varied depending on the plant developmental stages (Kirby and Faris 1972). Also tiller ears that reach maturity markedly later than the main culm ear itself decrease the grain yield quality and complicate the harvest (Peltonen-Sainio et al. 2009). However, the tillers have also been observed to have various benefits for temperate cereals. The tillers increased the ground coverage and the LAI at the early stages of growth, which eases the competition against the weeds and adds to the total photosynthetic area (Jewiss 1972, Lemerle et al. 1996, Peltonen-Sainio et al. 1997). The increase of LAI above the optimum levels, however, is not beneficial to the plant as the respiration and shading increases and affects the accumulation of dry-matter (Peltonen-

Sainio et al. 1997). The tillers also acted as a compensatory measure in case of the main culm failure (Cannell 1969a, Alaoui et al. 1988).

The role of coleoptile tillers in the grain yield formation has long been under debate (Cannell 1969a, Rawson 1971, Rebetzke et al. 2008). On barley, Cannell (1969a) considered the coleoptile tiller ear to contribute sufficiently to the final grain yield, although its significance was lesser than the ears of main culm and first main culm tiller. Rawson (1971) reached similar conclusions regarding coleoptile tiller on wheat as Cannell (1969a) on barley. Rawson (1971) stated that the role of coleoptile tiller in final grain yield is questionable and thus wheat varieties without coleoptile tiller would yield higher grain yields per unit area. However, Rebetzke et al. (2008) concluded that the importance of coleoptile tiller on the size of the final grain yield depends on wheat genotype and the environmental factors in the production area. All the conventional tillering accessions used in this study produced coleoptile tillers apart from some exceptions, but fewer in numbers than the T1 tillers. Coleoptile tillers initiated first and survived the longest.

Balkema-Boomstra and Mastebroek (1993) observed that the uniculm barley accessions, grown in West-European conditions, did not perform evenly with the conventional tillering barley accessions under favorable growing conditions. However, uniculm growth habit has been suggested to be a beneficial trait in the marginal production areas, such as the northern latitudes, where environmental conditions during growing season favour the late developing tillers (Balkema-Boomstra and Mastebroek 1993, Peltonen-Sainio et al. 2009). To avoid the formation of late developing tillers, it has been a common practise in Finland to increase the sowing density so that no tillers develop in the crop stand (Peltonen-Sainio et al. 2009).

Dofing (1996) compared uniculm and conventional tillering barley performance on field conditions in Alaska, US. The uniculm plants had faster development and more uniform maturity than the conventional tillering barley accessions, but the final grain yield lagged behind the conventional tillering accessions (Dofing 1996). Mäkelä and Muurinen (2012) similarly concluded that the grain yields in the uniculm accessions were smaller than in the conventional tillering accessions, although the stability of the uniculm accessions' yields were more pronounced.

Mäkelä and Muurinen (2012) observed that the uniculm accessions had higher reserves of water-soluble carbohydrates in their leaves, nodes and internodes, among other plant parts, than their conventional tillering counterparts on Finnish field conditions. As the uniculm accessions in this study had more and larger leaves on the main culm than the conventional tillering accessions, it could be hypothesized that those accessions would have had more reservoirs of water-soluble carbohydrates. However, Mäkelä and Muurinen (2012) concluded that the uniculm growth habit would not provide additional gains, since the uniculm barley accessions were unable to remobilize the assimilates to the grains, and the yields were smaller than in the conventional tillering accessions. The conventional tillering accessions, in turn, could remobilize the additional assimilates gained via increased LAI in the tillers (Mäkelä and Muurinen 2012). The ability to remobilize the assimilates to the grains is especially important under abiotic stress during the grain filling phase.

The spikes of uniculm barley accessions are known to have abnormalities that negatively affect the yield realization (Kirby 1973, Dofing 1996). These abnormalities are often linked to the uniculm growth habit as number of genes related to tiller formation, such as mutated genes *uc*$_2$ and *als*, result also in abnormalities in the development of inflorescence (Dofing 1996, Dabbert et al. 2009). No measurements of spike abnormalities were made in this experiment, although it would have been likely for some of such changes to occur. However, it should be taken into account that uniculm accessions used in this and previous studies have not been specifically cultivated for the higher grain yield production (Dofing 1996).

7 CONCLUSIONS

The aim of this work was to investigate the effects of differing photoperiods on barley leaf and tiller growth. As was hypothesized, the long photoperiod reduced the individual leaf size and main culm leaf area. The plant growth and the leaf and tiller emergence rates all were faster in the long photoperiod, as was expected. However, contrary to the hypothesis, the number of tillers increased in the long photoperiod.

The other aim was to compare the differences between growth habit as well as the row-type effects on leaf and tiller growth. The uniculm accessions had larger leaves and main culm leaf area than the conventional tillering accessions. The leaf emergence rates were also faster in the uniculm plants than in the conventional tillering plants. Differences between the two row-types were more pronounced than what was hypothesized. Generally, the six-rowed accessions had larger leaves and main culm leaf area than the two-rowed accessions, as was expected. The two-rowed accessions, in turn, had a higher tiller emergence rate and tiller number than the six-rowed accessions. As an exception to previous knowledge, the leaf emergence rate showed no differences among the two row-types, although two-rowed accessions tended to have higher leaf emergence rates than the six-rowed accessions.

The experiments shed new light on the effects of long photoperiod, phenomenon naturally occurring in the northern latitudes, to the barley leaf and tiller growth. The Nordic accessions had smaller leaf areas, which in high plant densities will minimise the shading effect of the neighbouring plants in the crop stand. The tiller emergence rates of the Nordic accessions were also faster than the tiller emergence rates of the other accessions originating from North America and Central Europe. In other words, the Nordic accessions are cultivated to perform well under the challenging Nordic conditions. The uniculm accessions did not provide any notable benefits over the conventional tillering accessions in northern latitude conditions. Thus, the uniculm accessions still need further improvements to prove their worth in actual agricultural production.

In conclusion, this work revealed intriguing differences between various barley accessions and provided a basis for further investigations on the subject. For future studies, it would be worth to further investigate the genes affecting both tillering and spike development in uniculm accessions, and to cultivate and assess the performance of uniculm accessions with higher grain yields. This would enable fairer comparison of the performances between uniculm and conventional tillering accessions in actual agricultural production.

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